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Determinants of native avian richness in suburban remnant vegetation: Implications for conservation planning

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1. Introduction

In recent decades, the impacts of urbanization have been recognized as a key threat to many natural ecosystems around the world (e.g. Rottenborn, 1999; Eppink et al., 2004). Urbanization results in fundamental changes to landscape composition and configuration with significant impacts upon the fauna and flora living within urban landscapes (Cornelis and Hermy, 2004; Clergeau et al., 2006a). These changes can either occur in landscapes that were already substantially modified (e.g. agricultural areas) and also areas that were relatively natural (e.g. forests and woodlands). While some urban areas are likely to represent highly simplified and homogenous landscapes (e.g. inner city areas (Fernández Juricic, 2000)), other urban areas can be viewed as variegated landscapes (cf. Ford and Barrett, 1995; McIntyre and Hobbs,

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1999) which are complex in structure, being comprised of integrated zones of residential development, industrial areas, remnant native vegetation patches and corridors, and open space. The pattern of urban landscapes (i.e. landscape composition and configuration) is expected to have a strong influence on the ability of wildlife to persist in urban areas (e.g. Dunford and Freemark, 2004; Platt and Lill, 2006; White et al., 2005; Pidgeon et al., 2007). While urban areas are increasingly recognized as having potential value for biodiversity conservation (Fernández Juricic and Jokimäki, 2001; Bryant, 2006; Pacheco and Vasconcelos, 2006), the relationship between biodiversity and the structure and configuration of the urban landscape is poorly understood.

Most recent research examining the influence of urbanization on biodiversity has utilized birds as a model group (see Chance and Walsh, 2006). Several common themes have subsequently emerged from this research largely relating to the simplification and change in avian community structure generally referred to as biotic homogenisation (e.g. Clergeau et al., 2006b). Species common in urban landscapes tend to be either exotic invaders or generalist native species that are tolerant of a wide variety of urban conditions (e.g. White et al., 2005; Antos et al., 2006; McKinney, 2006). Urban environments also often exhibit a high abundance of birds, but this can be tempered by low species richness, particularly of indigenous native species. Within urban environments, patches of remnant vegetation have been demonstrated to support a greater species richness and abundance of birds compared to surrounding residential areas (Fernández Juricic and Jokimäki, 2001; White et al., 2005). Of particular importance are patches of remnant vegetation, which appear to be critical for maintaining assemblages of indigenous birds in urban areas (Catterall et al., 1991; Recher, 2004; White et al., 2005).

One of the major issues for urban planning and conservation managers alike is a general paucity of ecological information to inform sound planning decisions. McKinney (2006) highlights the need to develop strategies to preserve indigenous species in urbanized landscapes. To develop such strategies we need an improved understanding of how indigenous species respond to urbanization processes and of the drivers of the distribution of indigenous species (Whited et al., 2000).

Remnant indigenous vegetation offers the best starting point to conserve native bird communities in urban environments, but even in remnant vegetation there are considerable differences in the representation of indigenous species (e.g. White et al., 2005; Jokimäki, 1999; Tilghman, 1987). What, therefore, drives native species composition in urban remnant vegetation? Are the responses of different types of species different? And how can this information be used to better plan urban environments to maintain maximum native species richness? We examine the major determinants of native bird species presence and richness in native vegetation remnants in urbanized environments in Melbourne, Australia. Specifically, we aim to determine whether remnant size is the major determinant of species diversity or whether other habitat or landscape variables, such as vegetation structure and extent of surrounding vegetation, are also important. The responses of ecological groups of birds (based on habitat preference, foraging strata and life history attributes) to these landscape and habitat variables are examined. Recommendations to help urban planners maintain and enhance native bird species richness in urban environments are provided.

2. Methods

2.1. *Study area*

Research was conducted within the metropolitan region of Melbourne, Australia (37°50′S, 44°58′E), which has a human population of around 3.5 million. Despite this large population, housing density is low medium (population density 468 persons/km^2 in 2004; ABS, 2006), and consequently a large urban sprawl has developed. Significant increases in the number of multi unit dwellings have occurred in recent years and consequently housing density is increasing (Buxton and Tieman, 2005). A wide range of natural vegetation types occurred prior to settlement including forests, woodlands, heathlands, wetlands and grasslands. Remnants of many of these habitats may still be found within parks and reserves embedded in the urban matrix. We define the ‘urban matrix’ as all areas of the urban environment that are not patches of remnant vegetation. The urban matrix, therefore, includes residential housing (both single and multi unit dwellings), industrial areas and urban infrastructure such as streets, community facilities and open space (e.g. golf courses, sports grounds). We focused our study only on indigenous woodland vegetation (i.e. vegetation dominated by trees) which is the dominant type of vegetation, remaining mostly in sites managed to retain this vegetation and which receive only low passive recreational use. Other non woodland vegetation types in the Melbourne area such as heaths, grasslands and wetlands tend to support different bird communities and would not have been comparable with woodland vegetation. All study sites were dominated by evergreen species (mainly of the genus *Eucalyptus* although the genera *Acacia*, *Leptospermum* and *Melaleuca* occurred as co dominants in some areas) and consisted of original native vegetation that had not been cleared. A few of the study sites also contained areas of re planted indigenous vegetation, but none were dominated by it. All study sites were located within the Gippsland Plain bioregion, in the eastern and southeastern suburbs, within a 30 km radius of the Melbourne Central Business District.

Remnants were selected based on size and availability. Remnants were divided into three size classes small (1 5 ha) (n 15), medium (6 15 ha) (n 14) and large (>15 ha) (n 10). All sites were at least 2 km apart to improve their spatial independence (Fig. 1).

2.2. *Bird surveys*

One hectare transects (200 m × 50 m) were used to assess the avian species richness of each remnant. The number of transects at a site was stratified according to remnant size; one transect was used to survey small remnants, two transects were used in medium remnants and three transects were used in large remnants. Multiple transects were used because we were investigating richness at the remnant level and not the transect level per se. Multiple transects also helped to

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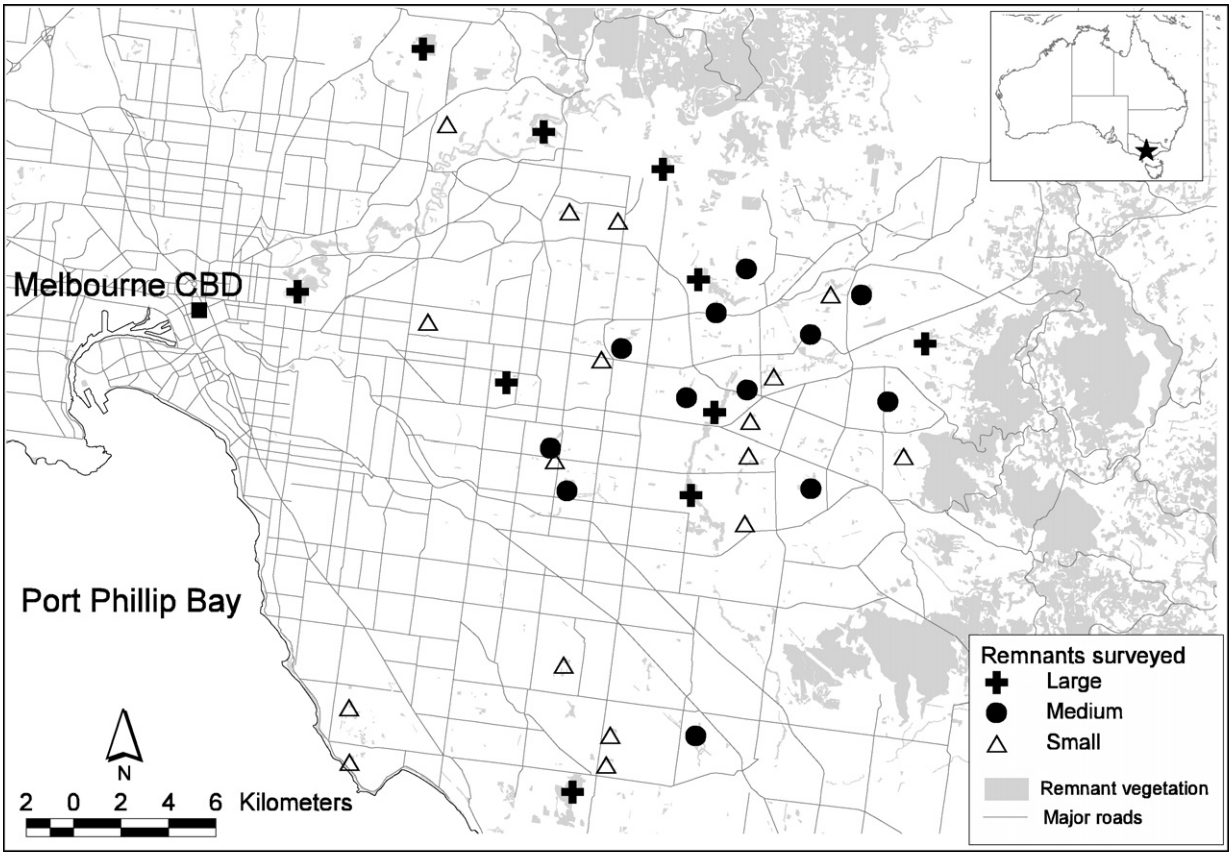

Fig. 1 – Locations of all study sites in the suburban zone of Melbourne, Australia.

account for greater habitat and structural heterogeneity which occurred in the larger reserves. Habitat and structural heterogeneity needs to be sampled adequately to provide an accurate assessment of bird species richness within a rem nant. Transects were located away from the edges of the rem nants where possible. Surveys were conducted during the non breeding season (April July) of 2003 and breeding season (October February) of 2003/04. Each transect was surveyed four times in each season, on different days, between dawn and midday during favourable conditions (days of high wind or rain were avoided). The multiple transects within medium and large remnants were surveyed on the same day. All sur veys were conducted by experienced bird observers (M.J.A., J.A.F., G.C.P.).

Each transect was traversed over a 10 min period and all birds seen and heard within the bounds of the transect were recorded, including those flying above the canopy. The results from all transects within a remnant were then pooled to pro vide an indication of the richness of each remnant. Nocturnal surveys were not undertaken and therefore species active at night (e.g. owls) were poorly sampled. Aquatic birds, intro duced birds and presumed aviculture escapees were excluded from consideration in this paper.

Species were classified into a series of ecological groups based on resilience to urbanization, foraging location and migratory status (Table 1). Species were also classified into landscape response groups based on findings from a previous study where bird communities were surveyed within the ur ban matrix (streetscapes) as well as within remnant vegeta tion (see White et al., 2005). Matrix tolerant species were defined as those species found in >5 of the 27 streetscape sites used in White et al. (2005). Remnant reliant species were those found in ⩽5 of the 27 streetscape sites used in White et al. (2005). Bird species were assigned to foraging groups based on a combination of previous assessments and pub lished information (e.g. Recher and Holmes, 1985; Ford et al., 1986; Mac Nally, 1994,1996; Loyn, 1998; Tzaros, 2001), and observations made by the authors and the opinion of ex perts. The species were also categorized into migrant groups (migrant, partial migrant or non migrant) based on the large scale movement patterns described by Griffioen and Clarke (2002) from analyses of the Atlas of Australian Birds database for southeastern Australia.

2.3. *Habitat measures*

Habitat assessments were conducted at each site. Four 20 m × 20 m quadrats were established at 50 m intervals along each bird survey transect. The results across all quadrats within a particular remnant were averaged. Measures were taken of canopy cover and also different ground cover attri butes, including the number of logs and the % cover of leaf lit ter, bare ground, native grasses and herbs within each quadrat. Measures were also taken of the % cover of low shrubs up to 1.5 m and tall shrubs between 1.5 m and 3 m within each quadrat. A geographical information system

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Table 1 – Bird species recorded in urban remnant vegetation in Melbourne, and predominant foraging location, migratory status and tolerance of urban matrix

Common name	Species name	Foraging location	Migrant status	Matrix tolerance*
Common bronzewing	*Phaps chalcoptera*	G	N	n
Crested pigeon	*Ocyphaps lophotes*	G	N	n
Tawny frogmouth	*Podargus strigoides*	G	N	n
Whistling kite	*Haliastur sphenurus*	G	N	n
Collared sparrowhawk	*Accipiter cirrhocephalus*	C	N	n
Little eagle	*Hieraaetus morphnoides*	G	N	n
Nankeen kestrel	*Falco cenchroides*	G	N	n
Australian hobby	*Falco longipennis*	C	N	n
Yellow tailed black cockatoo	*Calyptorhynchus funereus*	C	P	n
Gang gang cockatoo	*Callocephalon fimbriatum*	C	M	n
Galah	*Eolophus roseicapillus*	G	N	n
Long billed corella	*Cacatua tenuirostris*	G	N	n
Little corella	*Cacatua sanguinea*	G	N	n
Sulphur crested cockatoo	*Cacatua galerita*	G	N	n
Rainbow lorikeet	*Trichoglossus haematodus*	C	N	y
Musk lorikeet	*Glossopsitta concinna*	C	P	y
Little lorikeet	*Glossopsitta pusilla*	C	P	n
Australian King parrot	*Alisterus scapularis*	C	P	n
Crimson rosella	*Platycercus elegans*	C	N	n
Eastern rosella	*Platycercus eximius*	G	N	n
Swift parrot	*Lathamus discolor*	C	M	n
Red rumped parrot	*Psephotus haematonotus*	G	N	n
Shining bronze cuckoo	*Chalcites lucidus*	S	M	n
Pallid cuckoo	*Cacomantis pallidus*	S	M	n
Fan tailed cuckoo	*Cacomantis flabelliformis*	S	M	n
Powerful owl	*Ninox strenua*	C	N	n
Laughing kookaburra	*Dacelo novaeguineae*	G	N	n
Sacred kingfisher	*Todiramphus sanctus*	G	M	n
White throated treecreeper	*Corombates leucophaea*	C	N	n
Superb fairy wren	*Malurus cyaneus*	G	N	n
White browed scrubwren	*Sericornis frontalis*	G	N	n
White throated gerygone	*Gerygone albogularis*	C	M	n
Striated thornbill	*Acanthiza lineata*	C	N	n
Yellow thornbill	*Acanthiza nana*	C	N	n
Brown thornbill	*Acanthiza pusilla*	S	N	y
Spotted pardalote	*Pardalotus punctatus*	C	N	y
Striated pardalote	*Pardalotus striatus*	C	P	n
Eastern spinebill	*Acanthorhynchus tenuirostris*	S	P	y
Lewin's honeyeater	*Meliphaga lewinii*	C	P	n
Yellow faced Honeyeater	*Lichenostomus chrysops*	C	P	n
White eared honeyeater	*Lichenostomus leucotis*	C	N	n
White plumed honeyeater	*Lichenostomus penicillatus*	C	N	y
Bell miner	*Manorina melanophrys*	C	N	n
Noisy miner	*Manorina melanocephala*	C	N	y
Little wattlebird	*Anthochaera chrysoptera*	S	N	y
Red wattlebird	*Anthochaera carunculata*	C	P	y
New Holland honeyeater	*Phylidonyris novaehollandiae*	S	N	n
Brown headed honeyeater	*Melithreptus brevirostris*	C	N	n
White naped honeyeater	*Melithreptus lunatus*	C	P	n
Varied sittella	*Daphoenositta chrysoptera*	C	N	n
Black faced cuckoo shrike	*Coracina novaehollandiae*	C	P	n
Crested shrike tit	*Falcunculus frontatus*	C	N	n
Golden whistler	*Pachycephala pectoralis*	S	P	n
Rufous whistler	*Pachycephala rufiventris*	S	M	n
Grey shrike thrush	*Colluricincla harmonica*	S	N	n
Olive backed oriole	*Oriolus sagittatus*	C	M	n
Dusky woodswallow	*Artamus cyanopterus*	C	M	n
Grey butcherbird	*Cracticus torquatus*	S	N	y
Australian magpie	*Cracticus tibicen*	G	N	y
Pied currawong	*Strepera graculina*	C	P	n
Grey currawong	*Strepera versicolor*	C	P	n
Rufous fantail	*Rhipidura rufifrons*	S	M	n

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Table 1 – *continued*

Common name	Species name	Foraging location	Migrant status	Matrix tolerance*
Grey fantail	*Rhipidura albiscapa*	S	P	n
Willie wagtail	*Rhipidura leucophrys*	G	N	n
Australian raven	*Corvus coronoides*	G	N	n
Little raven	*Corvus mellori*	G	N	y
Satin flycatcher	*Myiagra cyanoleuca*	C	M	n
Magpie lark	*Grallina cyanoleuca*	G	N	y
Scarlet robin	*Petroica boodang*	G	P	n
Rose robin	*Petroica rosea*	S	M	n
Eastern yellow robin	*Eosaltrica australis*	G	N	n
Australian reed warbler	*Acrocephalus australis*	S	M	n
Silvereye	*Zosterops lateralis*	S	P	y
Welcome swallow	*Hirundo neoxena*	C	N	n
Tree Martin	*Petrochelidon nigricans*	C	M	n
Bassian thrush	*Zoothera lunulata*	G	N	n
Mistletoebird	*Dicaeum hirundinaceum*	C	P	n
Red browed finch	*Neochmia temporalis*	G	N	n

Aquatic birds, introduced species and presumed aviculture escapees were excluded. (Foraging location: G = ground, C = canopy, S = shrub; Migrant status: M = migrant, N = non migrant, P = partial migrant; Matrix tolerance: n = remnant reliant, y = matrix tolerant).

* Status determined from White et al. (2005), where a species found in >5 of the 27 streetscape sites was classified as matrix tolerant. Taxonomy follows Christidis and Boles (2008).

(ArcView GIS 3.3) was used to determine the size of each rem nant patch, the proportion of the remnant that was made up of riparian vegetation and the proportion of remnant vegeta tion within a 1 km radius of the surveyed remnant.

To reduce the number of habitat variables used in the anal ysis we derived two habitat complexity scores (Table 2). The first complexity score was for canopy and shrub complexity, and was derived from the data for canopy cover, low shrub cover and tall shrub cover (Table 2). The second complexity score was based on ground layer resources and included the % cover of leaf litter and native ground cover, and the number of logs per quadrat (Table 2). Spearman rank correlations were conducted to examine the relationship between each of the variables used to characterize the sites.

2.4. *Statistical analysis*

A two factor analysis of variance (ANOVA) was used to deter mine if species richness had stabilized over the eight survey visits to each remnant and across the three broad remnant size categories. Tukeys post hoc tests were used to identify differences within the ANOVA at an alpha level of 0.05.

To determine the relationships between the richness of native species within remnants and habitat variables, an information theoretic approach was taken, as described by Burnham and Anderson (2002). As this study had a relatively small sample size and the data were not overdispersed, the second order Akaike information criterion corrected for small sample sizes (AICc) was utilized. Generalized linear models using a Gaussian distribution were used to investigate the relationship between the total richness of species, matrix tol erant species, remnant reliant species, ground foraging spe cies, shrub foraging species, canopy foraging species, migrants, partial migrants and non migrants and a series of predictor habitat variables. The predictor variables applied in all analyses were the area (ha) of the remnant (Log10) (termed remnant area), the canopy/shrub complexity score, the ground complexity score, the proportion of a 1 km buffer around each remnant that consisted of remnant vegetation (termed % buffer remnant vegetation) and the proportion of the remnant that was comprised of riparian vegetation (termed % riparian vegetation).

Akaike differences (ΔAIC) were used to determine the level of support for each model in the candidate set. Burnham and

Table 2 – Contributors to habitat complexity scores

		Contribution to score				
		0	1	2	3	4
Contributors to canopy/shrub complexity score	Canopy cover	0 4.9%	5 19.9%	20 34.9%	35 49.9%	50+%
	Low shrub (0 1.5 m) cover	0 4.9%	5 14.9%	15 24.9%	25 34.9%	35+%
	Tall shrub (1.6 3 m) cover	0 4.9%	5 9.9%	10 14.9%	15 19.9%	20+%
Contributors to ground complexity score	Leaf litter cover	0 14.9%	15 29.9%	30 44.9%	45 59.9%	60+%
	Native ground cover	0 4.9%	5 19.9%	20 34.9%	35 49.9%	50+%
	Number of logs	0 2	3 7	8 11	12 17	18+

Scores were combined to produce a canopy/shrub complexity score and a ground complexity score.

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Anderson (2002) suggest that candidate models with Akaike differences less than 2 have substantial support as being the best of the candidate set of models. Akaike weights (ω_i) were additionally used to determine the evidence of support for each model. Akaike weights are the proportional weight of evidence in support of the particular model being the best model for the situation (Burnham and Anderson, 2002). Summed AIC weights were also used to help identify influen tial predictor variables in the models. The AIC weights are summed for all models that include a particular variable, with a highly influential variable being able to have a maximum weight of 1.

Model averaging was used to give un conditional model variances when the Akaike weight suggested no individual model was clearly the best ($\omega_i > 0.9$) (Anderson et al., 2001). Weighted model averaging based on 1000 bootstrapped sam ples was used to reduce model selection bias. Hierarchical partitioning was used to determine the independent contri bution of each predictor variable to the overall model. Models were developed using *R* statistical packages (Ihaka and Gen tleman, 1996), using algorithms to calculate AICc, bootstrap frequencies, and model averaged estimates (Scroggie, unpub lished). Hierarchical partitioning was undertaken in *R* using the hier.part package (Walsh and Mac Nally, 2003).

3. Results

The site based habitat and landscape variables differed con siderably across the 39 remnants. Remnant area ranged from 1 ha to 107 ha with a mean of 16.13 ha (±3.68 ha 1 SE). Canopy/shrub complexity scores ranged from 1 to 10 out of a possible 12, with a mean of 4.67 (±0.34 1 SE). Ground complexity scores ranged from 1 to 10 out of a possible 12, with a mean of 5.85 (±0.32 1 SE). The % buffer remnant vegetation ranged from 0% to 12%, with a mean of 2.99% (±0.46 1 SE). The % riparian veg etation ranged from 0% to 100% with a mean of 14.78% (±4.00% 1 SE). A series of Spearman rank correlations exam ined potential relationships between the site based variables. Even though we reduced the number of potential variables there were some relationships between the variables suggest ing some degree of co linearity. The % riparian vegetation was positively related to the size of the remnant (r_s 0.550, $P < 0.001$). The ground complexity score was positively corre lated with the canopy/shrub complexity score (r_s 0.518, P 0.001). The % buffer remnant vegetation was positively correlated with the size of the remnant (r_s 0.384, $P < 0.016$). The % buffer remnant vegetation was positively correlated with the % riparian vegetation (r_s 0.338, $P < 0.035$). The ground complexity score was positively correlated with rem nant area (r_s 0.323, $P < 0.045$).

Seventy nine native bird species were recorded during this study (see Table 1 for common and species names). A further six introduced species were also recorded. The response of introduced species to remnant characteristics has been re ported elsewhere (Antos et al., 2006), and they are not consid ered here. Species richness was effected by the size class of the remnant ($F_{(2,288)}$ 12.886, $P < 0.001$) with each increase in size class leading to an increase in species richness (Tukey $P < 0.05$). Species richness was also effected by the visit num ber ($F_{(7,288)}$ 239.488, $P < 0.001$). Species richness increased with each visit until the sixth visit (Tukey $P < 0.05$). There was no significant increase in richness detected between the sixth and eighth visits (Tukey $P > 0.05$) suggesting the sampling intensity was sufficient to lead to stabilized esti mates of species richness. There was no interaction between the size class of the remnants and the visit number ($F_{(14,288)}$ 0.990, P 0.464), suggesting that species accumula tion followed a similar pattern in different size class remnants.

3.1. *Total species richness*

A total of seven models were produced with delta AIC values <2, suggesting some evidence for multiple explanatory mod els (Table 3). The candidate sub set of models also had high R^2 values ranging from 0.664 to 0.695, and as such explained a large amount of the variation in the data. Weight ratios sug gest strong support for the first two models, but low Akaike weights for the main models suggest some model uncer tainty. Hierarchical partitioning and model averaging was conducted as no individual model was supported. Model aver aging showed strong support for a positive relationship be tween species richness and remnant area, with hierarchical partitioning also suggesting a strong independent contribu tion from remnant area (Table 4). Summed AIC weights also showed strong support for remnant area being included in any model (Table 4). The % riparian vegetation also had high independent contributions and summed AIC weights sug gesting some support for models including % riparian vegeta tion (Table 4). Overall, the total richness of species appears to be largely associated with remnant area and to a lesser extent the % riparian vegetation in the remnant.

3.2. *Matrix-tolerant and remnant-reliant species*

A total of 14 species were regarded as tolerant of the urban matrix (Table 1). The remaining 65 species were regarded as remnant reliant species. The richness of matrix tolerant spe cies was modeled against each of the predictor variables. There were five models with delta AIC values <2. However, very low R^2 values suggest that the models have limited explanatory power (Table 3). Model averaging suggested that remnant area may have a positive effect on the number of matrix tolerant species found in patches, but due to the ex tremely low R^2 values we consider this a weak response.

The richness of remnant reliant species was also modeled against each of the predictor variables. Five models were developed with substantial support to explain the richness of these species (Table 3). High R^2 values suggest strong explanatory power of each of the supported models. It was necessary to conduct model averaging as no one model had substantial support on its own. Model averaging suggests that the main contribution to the richness of remnant reliant spe cies was a positive relationship with remnant area (Table 4). Hierarchical partitioning indicated the remnant area had an independent contribution of 47.4%, adding further support to the importance of this factor. Further to remnant area, the % riparian vegetation had an independent contribution of 10.8% and moderate summed AIC weights.

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Table 3 – AIC_C based model selection for different ecological groups of species

	Model*	K	AICc	ΔAIC	Ranks	ω_i	i	R^2	ω_i/ω_j
Total species richness	Remnant area + % riparian vegetation	4	237.6	0.000	1	0.185	0.214	0.686	
	Remnant area	3	237.7	0.056	2	0.180	0.186	0.664	1.03
	Remnant area + canopy/shrub complexity	4	239.0	1.431	3	0.090	0.106	0.674	2.06
	Remnant area + canopy/shrub complexity + % riparian vegetation	5	239.1	1.494	4	0.088	0.114	0.695	2.10
	Remnant area + % buffer remnant vegetation	4	239.2	1.555	5	0.085	0.086	0.673	2.18
	Remnant area + % buffer remnant vegetation + % riparian vegetation	5	239.4	1.797	6	0.075	0.044	0.692	2.47
	Remnant area + ground complexity + % riparian vegetation	5	239.6	1.975	7	0.069	0.084	0.691	2.68
Matrix tolerant species	Remnant area	3	166.0	0.000	1	0.191	0.206	0.179	
	Remnant area + canopy/shrub complexity + ground complexity	5	167.0	0.758	2	0.131	0.242	0.266	1.46
	Remnant area + canopy/shrub complexity	4	167.0	1.285	3	0.101	0.144	0.204	1.89
	Remnant area + ground complexity	4	167.0	1.598	4	0.086	0.098	0.198	2.22
	Remnant area + % riparian vegetation	4	168.0	1.858	5	0.076	0.030	0.193	2.51
Remnant reliant species	Remnant area	3	225.6	0.000	1	0.207	0.248	0.673	
	Remnant area + % riparian vegetation	4	226.0	0.465	2	0.164	0.128	0.690	1.26
	Remnant area + % buffer remnant vegetation + % riparian vegetation	5	227.1	1.493	3	0.098	0.162	0.702	2.11
	Remnant area + % buffer remnant vegetation	4	227.3	1.713	4	0.088	0.098	0.680	2.35
	Remnant area + ground complexity	4	227.4	1.772	5	0.085	0.040	0.679	2.44
Ground foraging species	Remnant area	3	177.0	0.000	1	0.219	0.208	0.573	
	Remnant area + canopy/shrub complexity	4	178.0	0.327	2	0.186	0.230	0.596	1.18
	Remnant area + ground complexity	4	179.0	1.776	3	0.090	0.036	0.581	2.43
	Remnant area + % buffer remnant vegetation	4	179.0	1.987	4	0.081	0.070	0.579	2.70
	Remnant area + canopy/shrub complexity + % buffer remnant vegetation	5	179.0	2.011	5	0.080	0.102	0.606	2.74
Shrub foraging species	Remnant area + canopy/shrub complexity	4	163.0	0.000	1	0.306	0.250	0.519	
	Remnant area + canopy/shrub complexity + % riparian vegetation	5	164.0	1.140	2	0.173	0.114	0.537	1.77
	Remnant area + canopy/shrub complexity + % buffer remnant vegetation	5	164.0	1.640	3	0.135	0.104	0.531	2.27
	Remnant area + canopy/shrub complexity + ground complexity	5	165.0	1.980	4	0.114	0.090	0.527	2.68
	Remnant area + canopy/shrub complexity + ground complexity + % riparian vegetation	6	165.0	2.380	5	0.093	0.074	0.555	3.29
Canopy foraging species	Remnant area + % riparian vegetation	4	186.0	0.000	1	0.243	0.260	0.583	
	Remnant area	3	186.0	0.173	2	0.223	0.246	0.554	1.09
	Remnant area + ground complexity	4	188.0	2.431	3	0.072	0.090	0.556	3.38
	Remnant area + canopy/shrub complexity + % riparian vegetation	5	188.0	2.476	4	0.071	0.076	0.585	3.42
	Remnant area + canopy/shrub complexity	4	188.0	2.493	5	0.070	0.078	0.556	3.47
Migrants	Remnant area	3	126.0	0.000	1	0.203	0.120	0.305	
	Remnant area + % buffer remnant vegetation	4	126.0	0.131	2	0.190	0.208	0.346	1.07
	Remnant area + canopy/shrub complexity + % buffer remnant vegetation	5	128.0	1.671	3	0.088	0.084	0.364	2.31

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Table 3 – *continued*

	Model*	K	AICc	ΔAIC	Ranks	ω_i	i	R^2	ω_i/ω_j
	Remnant area + % riparian vegetation	4	128.0	1.889	4	0.079	0.044	0.316	2.57
	Remnant area + canopy/shrub complexity	4	128.0	1.905	5	0.078	0.136	0.316	2.60
	Remnant area + % riparian vegetation + % buffer remnant vegetation	5	128.0	1.945	6	0.077	0.106	0.360	2.64
Partial migrants	Remnant area + canopy/shrub complexity	4	174.0	0.000	1	0.315	0.406	0.501	
	Remnant area	3	176.0	1.650	2	0.138	0.204	0.445	2.28
	Remnant area + canopy/shrub complexity + % riparian vegetation	5	176.0	2.470	3	0.092	0.038	0.503	3.42
	Remnant area + canopy/shrub complexity + % buffer remnant vegetation	5	176.0	2.590	4	0.086	0.024	0.502	3.66
	Remnant area + canopy/shrub complexity + ground complexity	5	176.0	2.640	5	0.084	0.080	0.501	3.75
Non migrants	Remnant area + % riparian vegetation	4	211.0	0.000	1	0.347	0.370	0.626	
	Remnant area	3	213.0	2.120	2	0.120	0.172	0.579	2.89
	Remnant area + ground complexity + % riparian vegetation	5	213.0	2.480	3	0.101	0.096	0.627	3.44
	Remnant area + % buffer remnant vegetation + % riparian vegetation	5	213.0	2.480	4	0.100	0.062	0.627	3.47
	Remnant area + canopy/shrub complexity + % riparian vegetation	5	213.0	2.480	5	0.100	0.124	0.627	3.47

Models based on the number of species present within each group at each site. Values represent the number of parameters (K), Akaike information criterion corrected for small sample sizes (AIC_C), AIC differences (ΔAIC), Akaike weights (ω_i), bootstrap selection frequencies (i) and regression explanation scores (R^2) for the best models and evidence ratios (ω_i/ω_j). The highest five models are provided. Extra models are provided if more than five models had a ΔAIC score of less than 2.

* Model variables include : remnant area = area of woodland patch in hectares (logged), canopy/shrub complexity score, ground complexity score, the percent of a 1 km buffer around each remnant patch that is made up of other remnant vegetation (% buffer remnant vegetation) and the percent of each remnant that is made up of riparian vegetation (% riparian vegetation).

3.3. *Foraging location*

Species were divided into categories based on their dominant foraging strata and substrates. Three broad foraging locations were identified, these being canopy, shrub layer and ground. Overall, 38 of the species recorded generally forage in the canopy, 16 in the shrub layer, and 25 on the ground (Table 1).

Models were developed examining the relationship between richness of ground foraging species and the five predictor variables. Four models were produced which had substantial support (Table 3). All the supported models included remnant area indicating the important role of remnant size. R^2 values suggest the models have the ability to explain reasonable amounts of variation. Model averaging suggests that a relationship between remnant area and canopy/shrub complexity may be important in determining the richness of ground foraging birds. High summed AIC values and high independent hierarchical partitioning contributions suggest that remnant area has a strong positive influence on the richness of ground foraging birds. Moderate summed AIC values also suggest that there is a negative relationship between canopy/shrub complexity and ground foraging species richness. Whilst canopy/shrub complexity has some importance it also has low independent contributions to the best model (Table 4). Hierarchical partitioning also suggests that the % riparian vegetation may have some influence, but the summed AIC weights do not support this. This indicates some degree of model uncertainty, but remnant area has a strong influential effect on the richness of ground foraging birds.

A total of four models had substantial support in explaining the richness of shrub foraging species (Table 3). All four supported models included remnant area and canopy/shrub complexity, suggesting these measures are important. The models derived had moderate R^2 values suggesting reasonable explanatory power. As no model had strong support as the best, a model averaging approach was taken. Model averaged coefficients suggest a positive relationship between the richness of shrub foraging species and remnant area and canopy/shrub complexity (Table 4). High summed AIC values and independent hierarchical partitioning contributions suggest that both these variables have a positive influence on the richness of shrub foraging birds.

Two models had substantial support in explaining the richness of canopy foraging species (Table 3). These two models indicated that either remnant area or remnant area in combination with the % riparian vegetation could explain the pattern observed. Moderate R^2 values suggest that the models have reasonable explanatory power. Model averaging still highlighted that the two previous models are the best to explain the patterns (Table 3). High summed AIC weights and an independent contribution of 49.6% in the hierarchical

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Table 4 – Model averaged coefficients, conditional and un-conditional standard errors, Z-scores and significance of each variable in each species richness model, and summed AIC weights (total AIC weight for each model including that variable)

Variable			Standard error					
		Coefficient	Conditional	Un conditional	Z	Pr(>lzl)	Contribution	Summed AIC weights
Total species richness	Remnant area	10.700	1.702	1.580	6.773	0.000	47.4	1.00
	Canopy/shrub complexity	0.111	0.433	0.249	0.444	0.657	0.7	0.304
	Ground complexity	0.043	0.486	0.211	0.203	0.839	2.5	0.234
	% Buffer	0.061	0.298	0.173	0.353	0.724	4.8	0.286
	% Riparian vegetation	0.029	0.037	0.032	0.930	0.352	11.3	0.498
Matrix tolerant species	Remnant area	1.334	0.675	0.572	2.330	0.020	42.6	0.890
	Canopy/shrub complexity	0.116	0.172	0.148	0.781	0.435	12.0	0.427
	Ground complexity	0.109	0.193	0.159	0.686	0.492	7.4	0.389
	% Buffer remnant vegetation	0.014	0.118	0.058	0.247	0.805	6.8	0.254
	% Riparian vegetation	0.003	0.015	0.009	0.347	0.729	12.2	0.296
Remnant reliant species	Remnant area	1.384	1.463	1.384	6.747	0.000	47.4	1.000
	Canopy/shrub complexity	0.170	0.372	0.029	0.172	0.863	0.4	0.236
	Ground complexity	0.262	0.418	0.127	0.485	0.628	4.1	0.307
	% Buffer remnant vegetation	0.149	0.256	0.050	0.336	0.737	4.4	0.268
	% Riparian vegetation	0.027	0.032	0.022	0.816	0.414	10.8	0.455
Ground foraging species	Remnant area	4.260	0.795	0.671	6.346	0.000	54.4	1.000
	Canopy/shrub complexity	0.126	0.202	0.152	0.826	0.409	3.3	0.441
	Ground complexity	0.015	0.227	0.104	0.142	0.887	1.5	0.249
	% Buffer remnant vegetation	0.031	0.139	0.083	0.366	0.714	5.9	0.278
	% Riparian vegetation	0.003	0.017	0.010	0.283	0.777	8.3	0.240
Shrub foraging species	Remnant area	1.732	0.634	0.652	2.658	0.008	20.7	0.984
	Canopy/shrub complexity	0.428	0.162	0.162	2.641	0.008	16.7	0.975
	Ground complexity	0.136	0.181	0.191	0.711	0.477	10.3	0.314
	% Buffer remnant vegetation	0.045	0.111	0.088	0.512	0.609	5.7	0.291
	% Riparian vegetation	0.012	0.014	0.015	0.789	0.430	9.0	0.390
Canopy foraging species	Remnant area	4.412	0.890	0.803	5.497	0.000	49.6	1.000
	Canopy/shrub complexity	0.024	0.227	0.108	0.223	0.823	0.4	0.231
	Ground complexity	0.025	0.254	0.122	0.202	0.840	1.4	0.228
	% Buffer remnant vegetation	0.001	0.156	0.057	0.024	0.981	3.0	0.212
	% Riparian vegetation	0.013	0.019	0.016	0.831	0.406	14.3	0.500
Migrants	Remnant area	1.137	0.407	0.360	3.153	0.002	48.2	0.988
	Canopy/shrub complexity	0.033	0.104	0.068	0.486	0.627	3.7	0.293
	Ground complexity	0.005	0.116	0.051	0.094	0.925	2.7	0.217
	% Buffer remnant vegetation	0.065	0.071	0.067	0.974	0.330	19.0	0.501
	% Riparian vegetation	0.002	0.009	0.006	0.343	0.732	3.4	0.276
Partial migrants	Remnant area	3.163	0.767	0.616	5.138	0.000	44.6	1.000
	Canopy/shrub complexity	0.191	0.195	0.163	1.177	0.239	6.1	0.649
	Ground complexity	0.027	0.219	0.120	0.225	0.822	4.5	0.245
	% Buffer remnant vegetation	0.007	0.134	0.053	0.124	0.901	3.9	0.218
	% Riparian vegetation	0.001	0.017	0.008	0.176	0.860	7.3	0.226
Non migrants	Remnant area	6.152	1.230	1.163	5.287	0.000	44.0	0.999
	Canopy/shrub complexity	0.020	0.313	0.127	0.160	0.873	0.2	0.220
	Ground complexity	0.013	0.351	0.138	0.096	0.924	1.8	0.218
	% Buffer remnant vegetation	0.014	0.215	0.091	0.157	0.876	3.7	0.223
	% Riparian vegetation	0.037	0.027	0.025	1.485	0.138	16.5	0.732

Results from hierarchical partitioning are shown, with the percentage independent contribution. See Table 3 for definition of model variables.

partitioning suggest that remnant area has a strong positive influence on canopy foraging species richness (Table 4). Lower independent contributions from the % riparian vegetation and reduced summed AIC weights suggest that this variable has less influence than remnant area on richness of canopy foraging species (Table 4).

3.4. *Migrant status*

Species were categorized based on their migratory status into the following groups migrant (15 species), partial migrant (18 species) or resident (46 species) (Table 1). A total of six models were produced which had support for explaining

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patterns in the richness of migrant species (Table 3). Whilst the models have limited explanatory ability (R^2 ranged from 0.305 and 0.364) the models all included remnant area along with other variables. As no one model was strongly supported as the best, model averaging was conducted. Model averaging suggested that the top model could include remnant area and % buffer remnant vegetation. A 48.2% independent contribution and a summed AIC weight of 0.988 (Table 4) suggests that remnant area is highly influential on the richness of migrant species. Further to this, an independent contribution of 19% and a moderate summed AIC weight suggests that % buffer remnant vegetation does have a moderate positive influence on the richness of migratory species (Table 4).

When examining the richness of partial migrants two possible explanatory models were produced from AIC. The top model included remnant area and canopy/shrub complexity (Table 3). Whilst this model had reasonable support (AIC weight 0.315) it was necessary to conduct model averaging. After model averaging the same model was the top model with a boot weight of 0.406 (Table 3). Remnant area was the strongest influencing factor (positive relationship) with an independent contribution of 44.6% and summed AIC weights of 1.000 (Table 4). The complexity of the canopy/shrub layer also had a positive influence on species richness, but to a lesser extent, with an independent contribution of 6.1% and summed AIC weights of 0.649 (Table 4).

Only one model was produced to explain the richness of non migrant species (Table 3). This model included remnant area and % riparian vegetation, but it had low AIC weights (Table 3), suggesting it may not be a good model to explain the patterns. Model averaging again supported this model as the most likely explanation of patterns in non migrant species richness (Table 3). Overall, there was a positive effect of remnant area and to a lesser extent % riparian vegetation. Remnant area had a 44.6% independent contribution and high summed AIC weights (Table 4). The % riparian vegetation had an independent contribution of 16.5% and high summed AIC weights (Table 4).

4. Discussion

The influence of remnant size on the occurrence and richness of various taxa has been well documented (e.g. Ambuel and Temple, 1983; Freemark and Merriam, 1986; Bennett and Ford, 1997; Abensperg Traun et al., 2000). Most studies have focused on agricultural systems, often where the surrounding matrix contrasts starkly with the remnant (e.g. cropland) (although see Park and Lee, 2000; Fernández Juricic and Jokimäki, 2001; Mörtberg, 2001; Smith, 2007, for examples from the Northern Hemisphere). Our study has demonstrated that remnant size is a key determinant of avian species richness in remnant vegetation (except for matrix tolerant species) within an urban context and a variegated landscape. While it has been previously determined that the structure and composition of bird assemblages differs between remnants of indigenous vegetation and the urban matrix (e.g. Parsons et al., 2003; White et al., 2005), our research also indicates that both landscape and structural characteristics can contribute to determining the species richness of individual remnants, but to a lesser extent than remnant size. Various aspects of the matrix may influence bird composition in woodland remnants by providing resources which enable persistence or movement between remnants or conversely, barriers or threats (e.g. Jokimäki and Huhta, 2000; Dunford and Freemark, 2004; White et al., 2005; Pidgeon et al., 2007).

All of the ecological groups of native bird species that we examined, except matrix tolerant species (i.e. generalist species), showed a strong and consistent positive association with remnant area (Table 5). The benefits of larger remnants to birds within the urban matrix are likely to be similar to those that have been proposed for agricultural systems. First, by sheer virtue of their size, larger remnants are more likely to support sustainable populations of species with more demanding resource requirements (e.g. top order predators). Second, larger remnants are more likely to contain greater habitat and environmental heterogeneity and thus provide suitable habitats for a wider array of species. Finally, larger patches support larger core areas which are less susceptible to edge effects such as increased temperature fluxes, weed invasion and the presence of predatory or parasitic species (Saunders et al., 1991; Antos and White, 2004).

As well as remnant size, another variable which made a positive contribution to explanatory models for most ecological groups of native bird species was the increasing proportion of riparian habitat (Table 5). Riparian zones provide high quality habitat for wildlife in the landscape (Catterall, 1993;

Table 5 – Relative strength of relationship between avian ecological groups and habitat variables based on an assessment of AIC outcomes and hierarchical partitioning

	Remnant area	Canopy/shrub complexity	Ground complexity	% Buffer remnant vegetation	% Riparian vegetation
Total species	Strong positive				Moderate positive
Matrix tolerant species	Weak positive				
Remnant reliant species	Strong positive				Weak positive
Ground foraging species	Strong positive	Weak negative			
Shrub foraging species	Moderate positive	Moderate positive			
Canopy foraging species	Strong positive				Moderate positive
Migrant	Strong positive			Moderate positive	
Partial migrants	Strong positive	Moderate positive			
Non migrants	Strong positive				Moderate positive

Blank cells = no detectable relationship.

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Palmer and Bennett, 2006). They are often characterized by increased productivity and greater structural complexity of vegetation when compared to surrounding non riparian areas in the landscape (Tzaros, 2001; Palmer and Bennett, 2006). In addition, riparian zones in urban landscapes com monly retain native vegetation in a linear corridor and potentially provide high vegetative connectivity and con duits for movement through the landscape. Riparian zones are mostly excluded from infrastructure development, espe cially on floodplains, and are often retained as corridors of open space in the urban matrix that often support native vegetation (Jim and Chen, 2003; Livingston et al., 2003; Find lay and Taylor, 2006).

Remnant reliant birds were strongly linked to large patches of remnant vegetation in the urban landscape. These birds are characteristic of forest and woodlands in southeastern Aus tralia (Loyn, 1985; Emison et al., 1987), but do not occur widely in the urban matrix outside of native vegetation patches (White et al., 2005). Small remnants (<2 ha) may be entirely composed of edge habitat (Forman et al., 1976) and therefore are likely to provide low value habitat for remnant reliant birds. This study has demonstrated that bird assemblages in small remnants are largely comprised of matrix tolerant spe cies which move freely between remnants and the urban ma trix and therefore are not sensitive to remnant size. The dependence of remnant reliant birds on relatively large areas of remnant vegetation makes them particularly vulnerable to extirpation from the urban environment as large areas of the urban matrix do not provide suitable habitat (White et al., 2005). Remnant reliant birds make a significant contribution to the richness of urban bird assemblages and therefore their conservation is important in maintaining urban biodiversity. Many remnant reliant species also contribute to remnant health by facilitating ecosystem processes such as pollination, insect control and the dispersal of certain plant species (e.g. Ford and Paton, 1986).

Group specific variations were evident and patch level characteristics were important for some ecological groups. For example, out of all foraging guilds, shrub foraging birds were least influenced by patch size alone and more influ enced by site characteristics (e.g. remnant area + canopy/ shrub complexity). This may indicate that vegetation struc ture (shrub density) is the key determinant of the presence of these species rather than remnant size. Generally, vegeta tion structure plays an important role in determining avian community structure in forested habitats (e.g. Willson, 1974; Gilmore, 1985).

Some long distance migrants, especially Neo tropical spe cies, can be more sensitive to remnant size than residents or partial (i.e. short distance) migrants (e.g. Ambuel and Temple, 1983). Many migratory species tend to decrease with increas ing urbanization (Beissinger and Osborne, 1982; Pennington et al., 2008). Our study found that migrants were positively influenced by the amount of other native vegetation within 1 km of the surveyed remnant, as well as by remnant size. The presence of nearby remnant vegetation may be impor tant by providing additional habitat and resources in the immediate vicinity that relatively mobile species are able to exploit. Surrounding native vegetation may also provide a more conspicuous visual cue for passing migratory species. Urban areas can also provide greater access to some key re sources for migratory or nomadic species, such as nectar from non indigenous flower sources (e.g. Fitzsimons et al., 2003; Smith and Lill, 2008), than would be available in natural areas.

4.1. *Implications for conservation*

Conservation and restoration of native vegetation in the ur ban environment is becoming more prevalent. There is a growing recognition that areas of high conservation value can be found within the urban matrix (Catterall et al., 1991; Park and Lee, 2000; Savard et al., 2000; Fernández Juricic and Jokimäki, 2001).

The research presented in this paper provides conserva tion managers and planners with a hierarchical process to re serve design and management in order to conserve the highest richness of remnant reliant native species within ur ban areas.

First, conservation efforts should preferentially focus on the retention of larger remnants of native vegetation, given that remnant area had such an overriding influence on spe cies richness. A focus should also be placed on increasing the size of existing remnant vegetation where possible. This may include strategic revegetation to increase existing rem nant size and/or connectivity with nearby remnants where practical. While this may be a difficult task in many older cit ies where space is limited (e.g. Fernández Juricic and Jok imäki, 2001), it can be a valid approach within newer cities, such as those in Australia, or within recently developed peri urban areas.

Second, where possible, riparian vegetation should be in cluded within reserves or, where it is already present, should be protected from further degradation and managed for con servation purposes to ensure its integrity. Riparian zones are an effective location to focus revegetation, restoration and conservation efforts in urban landscapes. Due to develop ment restrictions along waterways (e.g. flood zones etc.) and their attractiveness for recreational activities, networks of riparian zones are often retained in urban landscapes and, if managed appropriately, are likely to have a critical role in forming habitat networks for wildlife.

Third, efforts should be focused at maintaining levels of vegetation structure and complexity that will cater for a wide range of different bird species (e.g. shrub complexity for shrub foraging species) although our results indicate that focusing efforts on improving vegetation structure may not be an optimal allocation of resources if the remnant is small and isolated. Resources may be better spent in increasing the size and connectivity of remnants within the urban matrix.

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